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PHENOLOGY OF TROPICAL TREES FROM JARI, LOWER AMAZON, I. PHENOLOGY OF EIGHT FOREST COMMUNITIES

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ABSTRACT - Six classes of reproductive and vegetative phenologies of forest trees from eight different communities in the microregion of Jari were studied through 1508 individuals. Most trees flowered either during the dry season or during the transition dry-wet season, and fruited mainly during the wet season. The graphical displays obtained showed no significant difference in flowering and fruiting between the eight forest communities observed.

KEY WORDS: Plant reproduction, Reproductive phenology, Vegetative phenology, Tropical forest, Seasonality.

RESUMO - Seis categorias de fenologia vegetativa e reprodutiva de árvores de oito comunidades florestais da microregião do Jari foram estudadas em 1508 indivíduos. A maioria das árvores floresceu no final da estação seca ou entre esta e o início da estação chuvosa, e frutificou durante a estação chuvosa. Os gráficos obtidos não indicaram diferenças significantes de floração e frutificação entre as oito comunidades estudadas.

PALAVRAS-CHAVE: Reprodução de plantas, Fenologia reprodutiva, Fenologia vegetativa, Floresta tropical, Sazonalidade.

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INTRODUCTION

In the biology of higher plants no events seem more important than flowering and fruiting, since these structures are not only responsible for the genetic survival of the plant species but are also related to the biotic and abiotic environment. In plants, flowering patterns are linked not only to the timing, duration and frequency of flowering but also to the form of reproduction of each species. Vegetative phenology was also studied since it is important to evaluate the effects of the environment upon the forest communities. The Jari forests are semi-evergreen because most trees exhibit a great deal of leaf loss during the dry season (August to December).

Observational studies undertaken in the last two decades have shown distinguishable patterns in flowering and fruiting times occur among all ecosystems. Even tropical rain forests which do not experience major climatic changes throughout the year have a season when the rainfall is less pronounced. This, along with minor changes in photoperiod, are enough to cause variations in the reproductive and vegetative phases of trees. Appendix 1 gives the number of genera, species and trees involved in the study while Appendix 2 lists the 137 tree species studied whose flowering and fruiting phenologies can be found in Pires (1991). This paper summarizes the reproductive and vegetative phenologies of eight tropical forest communities through the summation of data from six phenological categories observed in 1508 trees of 137 tree species from Jari, lower Amazon.

THE STUDY AREA

The field work was carried out in an area between the rivers *Parú* and *Jari*, in the lower Amazon. These rivers are the two major easternmost tributaries on the northern bank of the *Amazon river* before it reaches the Atlantic ocean (Figure 1). The area studied is located in Pará and Amapá and its closest locality is the town of Monte Dourado (County of Almeirim) and a large area of the County of Mazagão (Amapá). Geographically the studied sites are close to the Equator, ranging from 0°27' to 1°6' Latitude South and 52°51' to 52°25' Longitude West.

The phenological study was carried out in eight sites of primary forest within reserves (Figure 1). All but one site belong to the Jari Company. It is the site Ibama, at the Jari Ecological Station. All sites are part of a complex of genetic reserves (The Jari Genetic Reserve), aimed to promote 'in situ' conservation of forest genetic resources, which the Jari Company implemented from 1984 through a cooperative agreement with the Brazilian National Genetic Resources Centre (CENARGEN), Brasília.



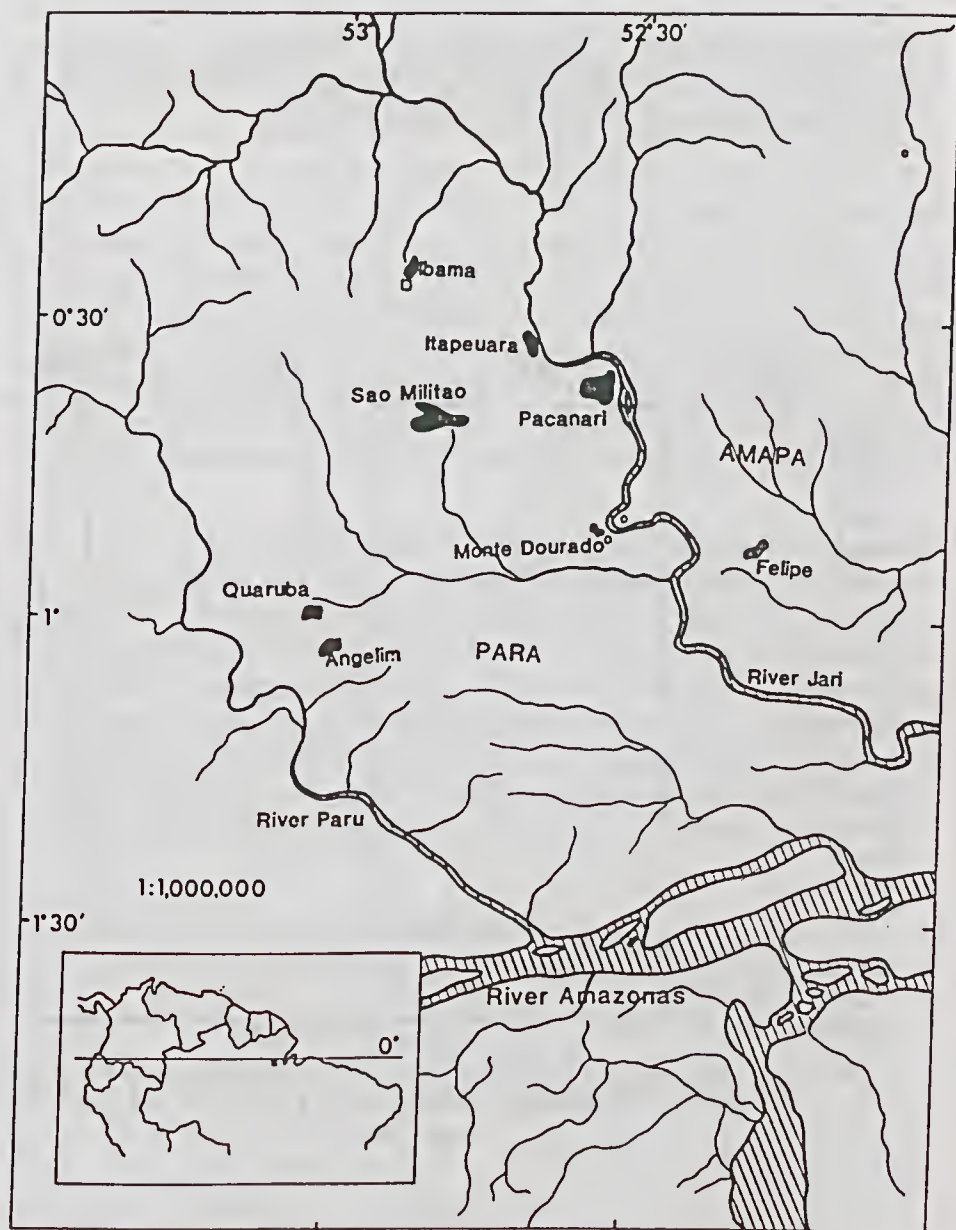


Figure 1 - Map of the Par -Jari microregion showing the eight forest sites studied.

The climate of Jari is hot and humid, with average temperature in the order of 26.4°C. The average yearly precipitation is 2,115 mm. This high precipitation average compensates for a mild dry season which takes place from August to December. The driest months, September to November, contribute with only 8 % of the annual volume of rain in the region (Figure 2).

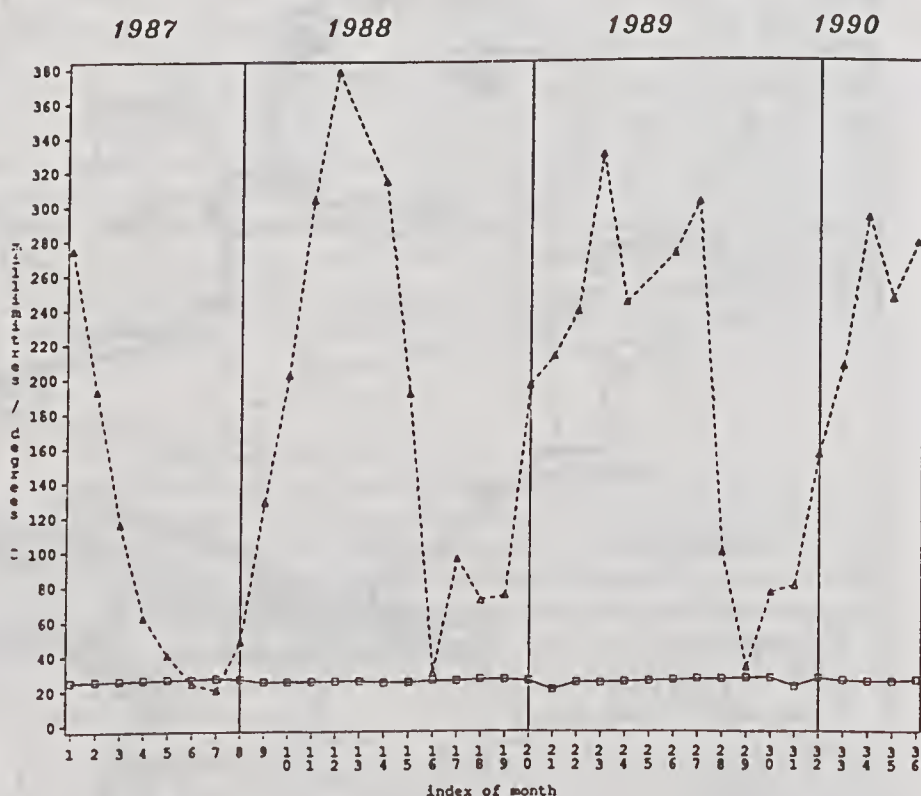


Figure 2 - Rainfall and temperature of the the Jari microregion during the course of the experiment.



METHODS

The 1508 trees included in this study constituted a subset of a larger statistical population of some nine thousand trees, which were identified during botanical surveys carried out by the author and assistants between 1985 and 1987 in the eight forest sites studied in the area of Jari. Figure 3a shows my assistant, Mr. Nilo T. Silva, observing a tree crown in one of the forests studied. The individuals selected for the phenological study were flagged to facilitate their relocation amongst the other trees of each reserve (Figure 3b). Their canopies were observed monthly with the aid of binoculars and the phenology phases were recorded in pre-prepared field data sheets. The observations covered 36 months, from May 1987 to April 1990. A system of nine codes was initially devised to facilitate the recording of the nine original phases. These were later simplified to six phases (Table 2) separated into two reproductive: flowering and fruiting and four vegetative: old canopy, leaf shedding, flushing and entire new canopy (Pires 1991).

The raw data of phenological codes attributed to each tree were stored and analysed in a personal XT computer through the program DBase III+ by Ashton-Tate. The resulting summation and proportions of the phenological data was transferred from PC diskettes into an Amdahl-5890 computer of the University of London Computer Centre, where they were analysed by means of the Statistical Analysis System (SAS), Version 5.18. In this paper the phenological data refer to the 36 monthly observations which took place from May 1987 to April 1990 (Table 1). The monthly indices used in the figures are displayed in Table 1. The symbols utilized in the same figures are listed in Table 2.

Table 1. Key to the monthly indices used in Figures

INDEX	MONTH	YEAR
1- 8	May-December	1987
9-20	January-December	1988
21-32	January-December	1989
33-36	January-April	1990



Table 2. Phenology phases recorded and key to the figure symbols

SYMBOL	PHENOLOGY PHASE
	Flowering
	Fruiting
	Old Canopy
	Leaf Shedding
	Flushing
	Entire New Canopy

RESULTS

1. Flowering and Fruiting

The combined flowering and fruiting phenologies of the 1508 trees from Jari investigated are displayed in Figure 4. Flowering occurred throughout the year but showed a distinct peak towards the end of the dry season. During the first year of the study (1987-88) the flowering peak occurred in January, which is normally the first month of the rainy season. That was not so in that particular year, when the dry season had extended until January. The overlap flowering of each of the eight forests studied is shown in Figure 5. Fruiting also occurred throughout the year but displayed a distinct peak during the rainy season, which in Jari goes from January to July (Figure 6). The fruiting peaks were more evident during 1987-88 and 1989-90 than in 1988-89.

In most of the trees investigated flowering lasted only a short period of time when compared with fruiting. For this reason flowering events sometimes passed undetected in the monthly observations of this study and can be inferred by the larger number of fruiting events as shown in Figure 4.

Flowering and fruiting were also calculated according to seasonal pattern of wet, dry, transition wet-dry and transition dry-wet (Table 3). Most trees flowered either during the dry season or between the end of the dry and beginning of the wet season. Fruiting occurred most often during the wet season and during the transition between the wet and the dry season. Very few species of trees fruited during the dry season (Table 3).

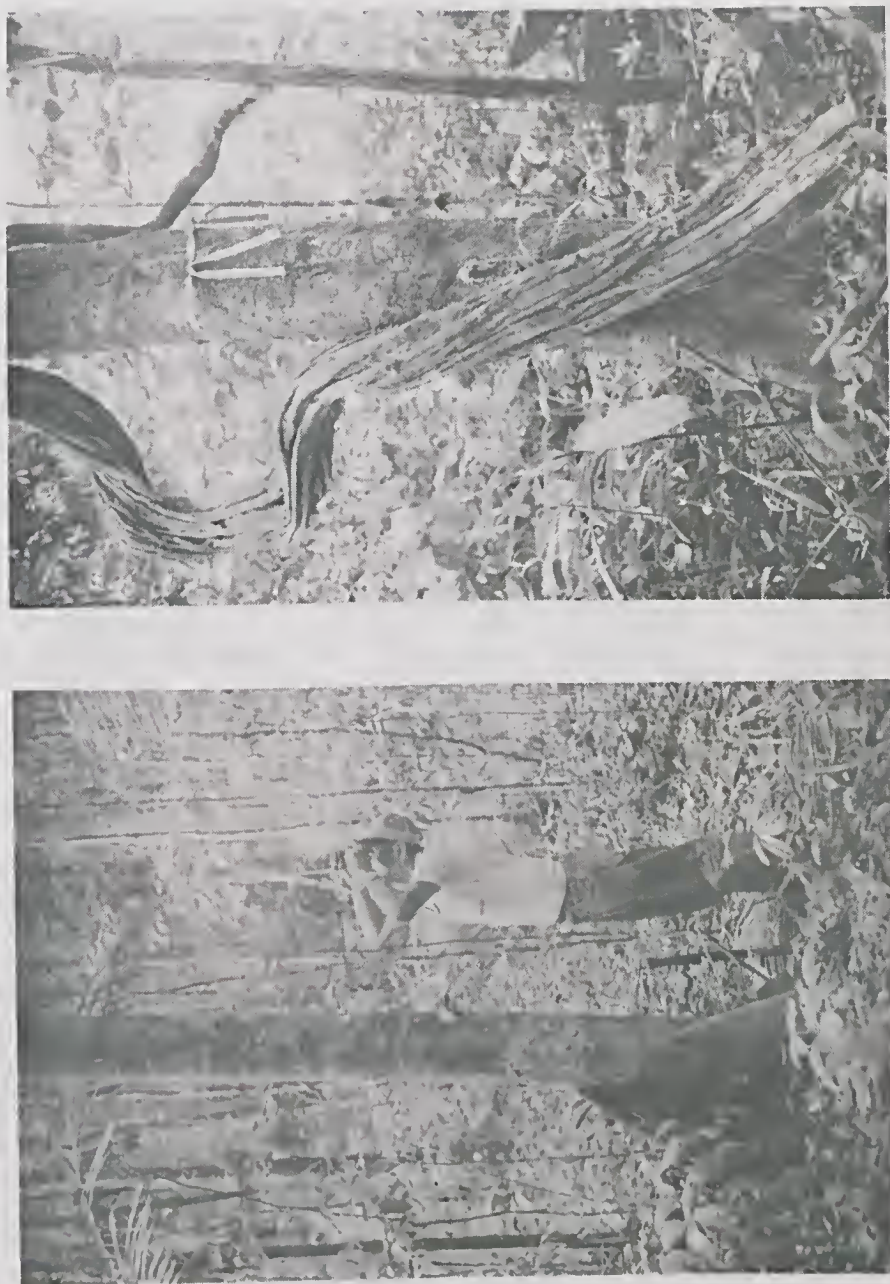


Figure 3 - A. Nilo T. Silva observing a canopy with binoculars; B. A marked tree of *Protium alisonii* at the IBAMA forest.

Table 3. Number of tree species flowering and fruiting in each separate or extended season.

SEASON	FLOWERING	FRUITING
Wet	16	59
Wet-Dry	12	12
Dry	38	9
Dry-Wet	72	53

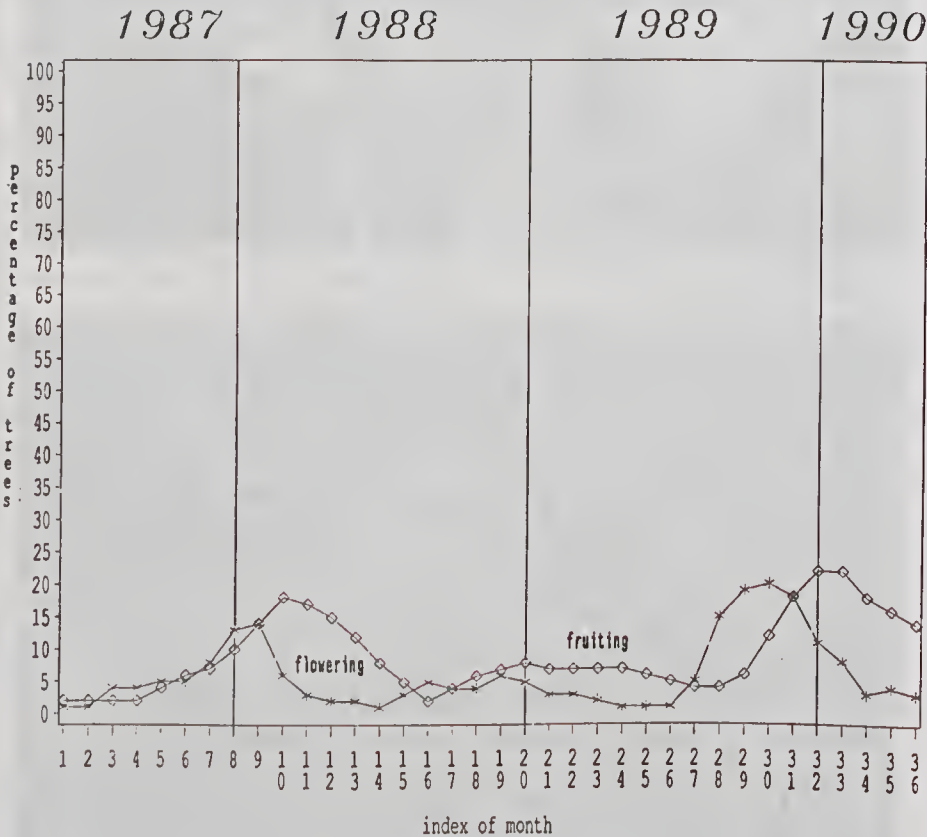


Figure 4 - Combined flowering and fruiting phenologies of the eight forest communities studied.

The variable most used in the phenology literature is the peak of flowering or fruiting events, which have been referred by some as 'mean' phenology. In this paper the peaks of flowering of each forest community studied were examined to check whether or not there was a significant difference between them. However, the median rather than the mean was used since the former is a more adequate measure of location for non-normally distributed data (Campbell 1989, Krebs 1989).

The overlaid fruiting of each of the eight forests studied is illustrated in Figure 6. Like the case of flowering (Figure 5) this figure indicates a clear superposition of the fruiting curves of all the forests studied. Figures 7 to 14 show the flowering and fruiting percentages of each of the eight forests studied. An examination of the peaks or median of fruiting of each forest community studied allowed to separate the peak months displayed in Table 4.

Table 4. Month of peak flowering and fruiting in the eight Jari forests studied.

Forest Community	Year:	87/88		88/89		89/90	
		Flo.	Fru.	Flo.	Fru.	Flo.	Fru.
Angelim (Ang)		Nov	Apr	no peak		Oct	Dec
Quaruba (Qua)		Jan	Feb	Nov	Mar	Nov	Dec
Monte Dourado (MtD)		Jan	Mar	Nov	Mar	Oct	Dec
Felipe (Fel)		Jan	Feb	no peak		Nov	Dec
São Militão (Sml)		Dec	Feb	no peak		Nov	Dec
Pacanari (Pac)		Dec	Mar	Nov	-	Nov	Jan
IBAMA (Iba)		Jan	Apr	no peak		Oct	Jan
Itapeuara (Ita)		Nov	Jan	Nov	Jan	Oct	Jan

It must also be emphasized that in Jari there were many trees which flowered but did not fruit. The combined flowering phenology of the eight native forests studied showed a maximum of 20 and a minimum of one percent of individuals flowering at any one month of the three years of observations.

2. Vegetative Phenology

The vegetative phenology of the microregion of rio Jari was inferred by combining the data from all 1508 trees observed (Figure 15). The vegetative phenologies of the forest sites studied were superimposed for visual comparison of the patterns (Figures 16 to 19). Flushing (Figure 16) was hardly observed since new leaves tended to appear gradually and mixed with existing old leaves.



Figure 17 shows the situation of old canopy in the eight forests studied. By comparing this figure with the rainfall of Jari during the same period (Figure 2) one can see the resemblance between the two. The illustration of the shedding condition (Figure 18) was the exact opposite to the old canopy condition shown in Figure 17 and coincided with the months that had the least rainfall (Figure 2). The phase entire new canopy is displayed in Figure 19. The seasonal climate found in the microregion of Jari apparently influences the shedding time of the trees observed by making it more pronounced during the dry season.

DISCUSSION

The major result of the present work was the uncovering of the small percentage of the individual trees flowering and fruiting even during the highest period of reproductivity activity of each community studied. In the eight native forests studied at Jari the average percentage of trees that entered the flowering stage at any one month was 20 per cent. The highest value, of 43 percent, occurred only at one of the dry open forests. The low fertility of tropical trees under primary forest condition has also been reported in French Guiana by Sabatier (1985) and by Mori & Prance (1987). The low proportion of flowering in the tree species studied can be interpreted as an adaptation to the stable environment found in the primary forest. In the primary forests studied many of the trees restricted their flowering to the sections of canopy that received direct sun light. The light factor, being limited a forest situation also favours a shift towards an investment in vegetative growth rather than in reproduction. An evidence for this is the fact that in Jari most, if not all, trees occurring near roads showed copious flowering and fruiting and seemed less tall than those individuals of the same species occurring in the forest. A problem needed to pursue further is to explain why so many trees flowered but not fruited. In some cases such as many species of *Meliaceae* a lower than expected fruit set is due to dioecism or even monoecism in which one of the sexes are non-functional. Although there has been an increase in the number of papers describing potential pollinators of tropical plants, observational and experimental studies on pollination mechanisms of tropical trees are still very few. For community ecology the reproductive behavior of trees can explain existing patterns of fruit set as well as the demography of each species within the forest.

The number of trees showing entire new canopy (Figure 19) is also interesting since it is a reflection of the environmental parameters of the microregion as a whole, which can be compared with other microregions within



the Amazon. As far as leaf shedding patterns are concerned the trees can be classified into three types. The most common type found in Jari involves those trees which shed only part of their canopies at a time, never becoming completely leafless. These trees are called semi-evergreen or semi-deciduous. Secondly, there are a small number of tree species which lose their entire canopy during the dry season. These are called deciduous even though their leafless condition lasts only a very short period. Examples of trees that exhibited deciduous behaviour at Jari are *Anacardium spruceanum*, *Tapirira* spp., *Eriotheca globosa*, *Parkia* spp., *Connarus perrottetii*, *Couratari guianensis* and some species of *Inga*. The third type are trees whose leaves are substituted gradually throughout the year, without a noticeable increase in shedding during the dry season. These are referred to as evergreen trees. Examples are *Tetragastris panamensis*, *Protium* spp., *Vantanea parviflora* and *Pentaclethra macroloba*. Finally, there are entire plant families which are more adapted to seasonal climate such as the Vochysiaceae and Humiriaceae. Species of these families occurred mainly in the two dry forests studied, Angelim and Quaruba. One of its common species, *Vochysia vismiifolia* shedded not only leaves but entire branches as well.

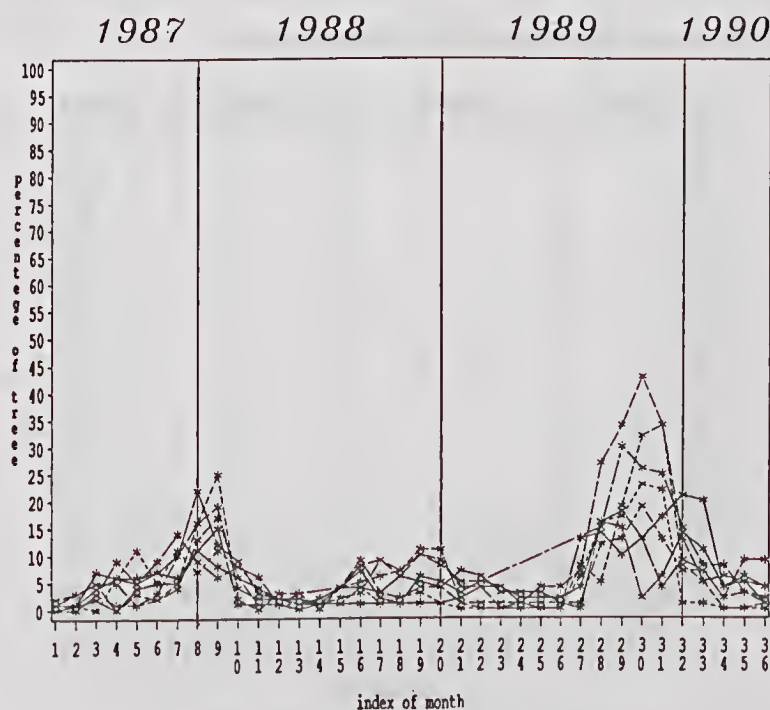


Figure 5 - Flowering phenology of the eight forest communities studied.

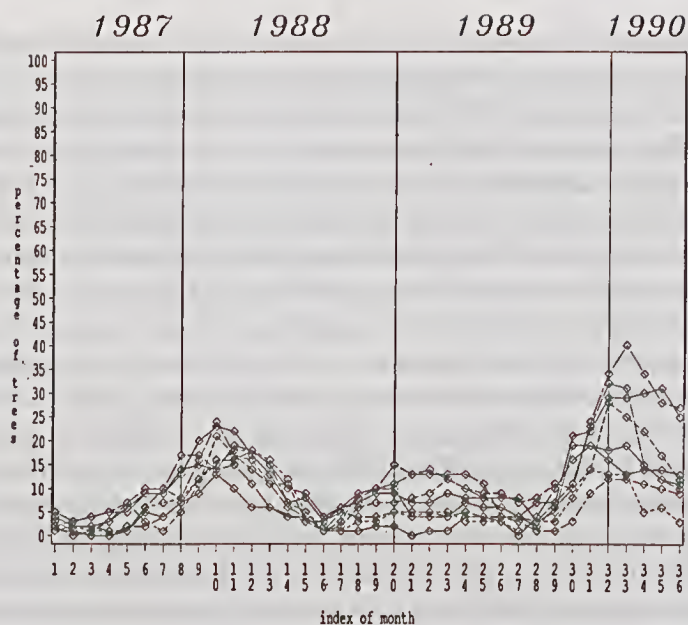
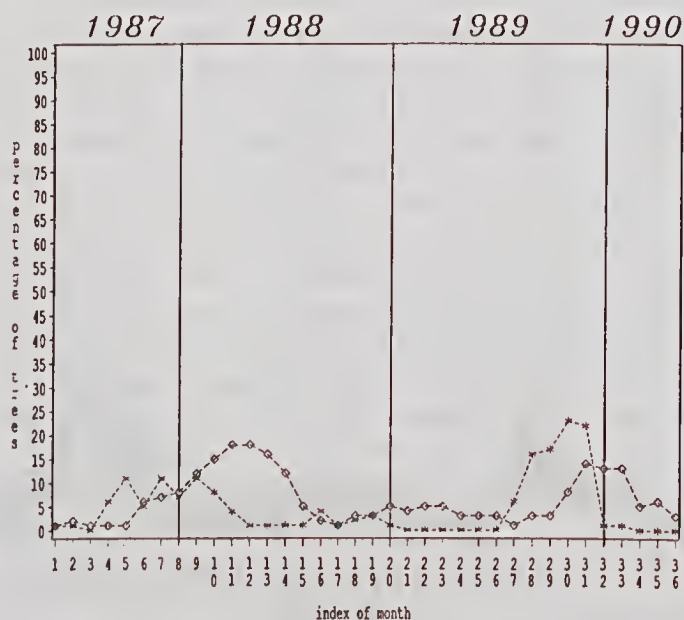
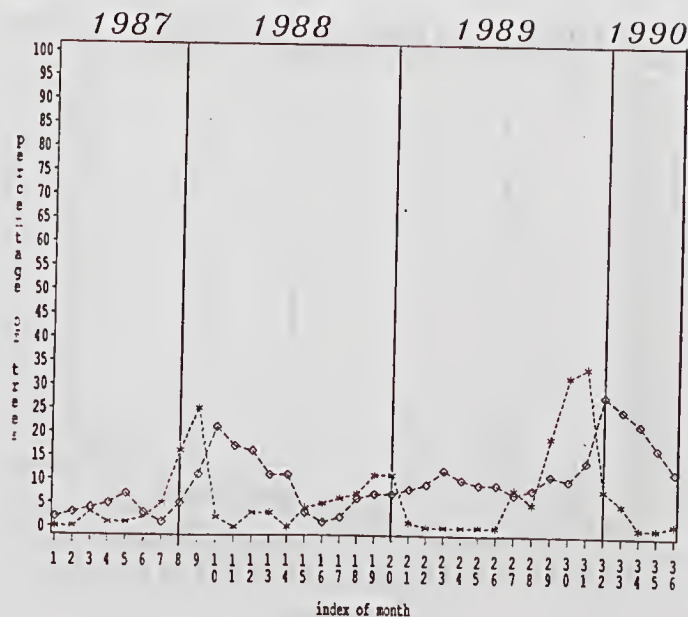


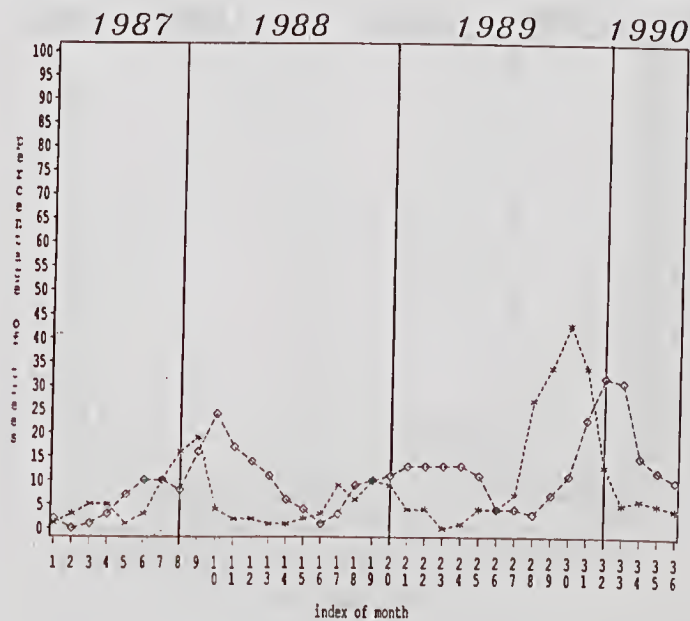
Figure 6 - Fruiting phenology of the eight forest communities studied.



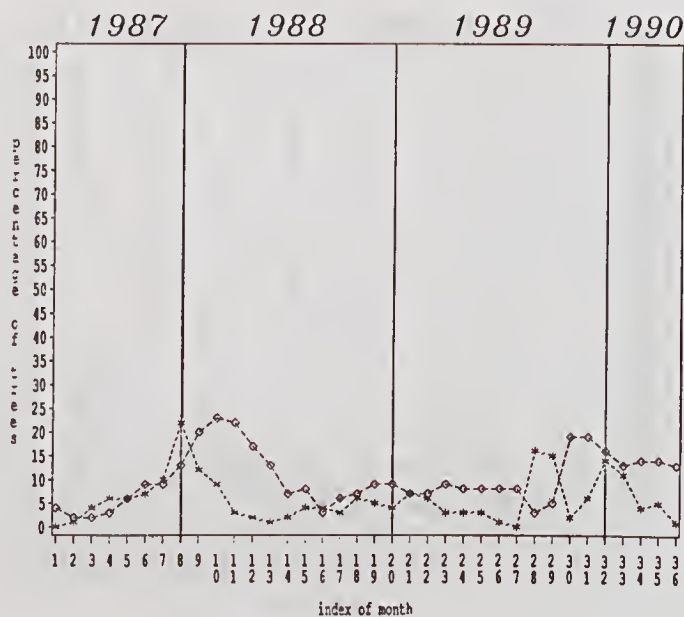
Figures 7 - Flowering and fruiting phenologies of the Angelim forest community.



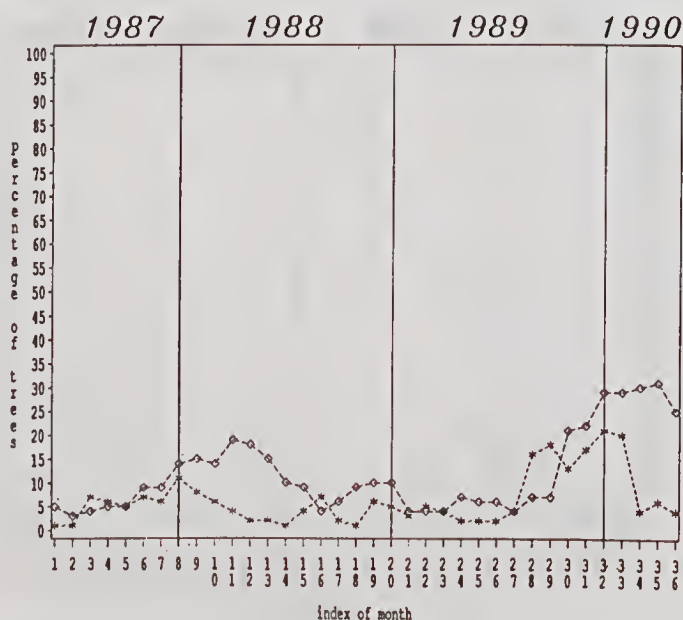
Figures 8 - Flowering and fruiting phenologies of the Quaruba forest community.



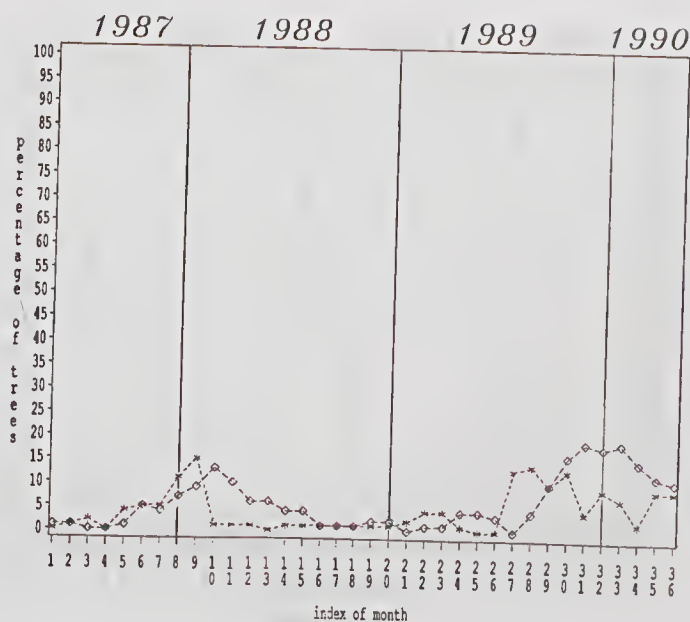
Figures 9 - Flowering and fruiting phenologies of the Monte Dourado forest community.



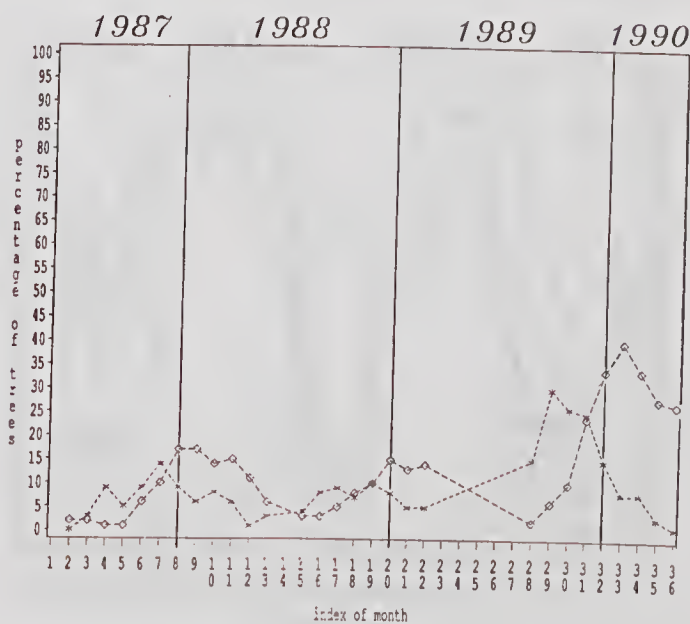
Figures 10 - Flowering and fruiting phenologies of the São Militão forest community.



Figures 11 - Flowering and fruiting phenologies of the Pacanari forest community.



Figures 12 - Flowering and fruiting phenologies of the Felipe forest community.



Figures 13 - Flowering and fruiting phenologies of the Itapecuara forest community.

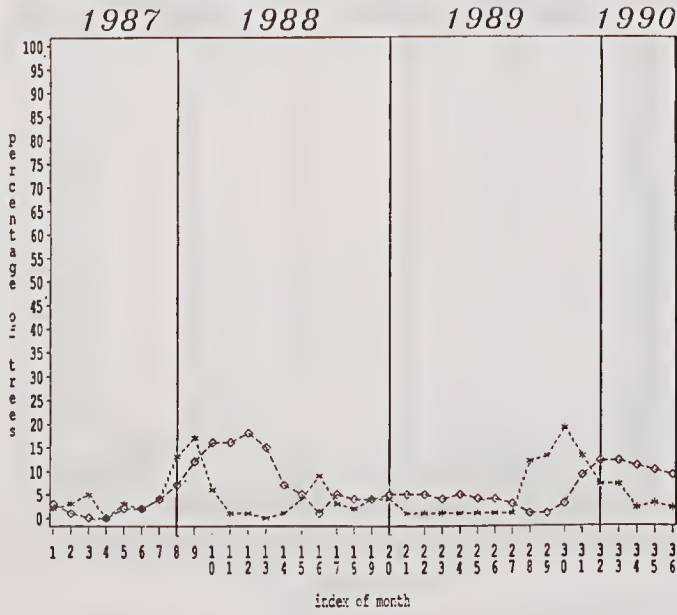


FIGURE 14 - Flowering and fruiting phenologies of the Ibama forest community.

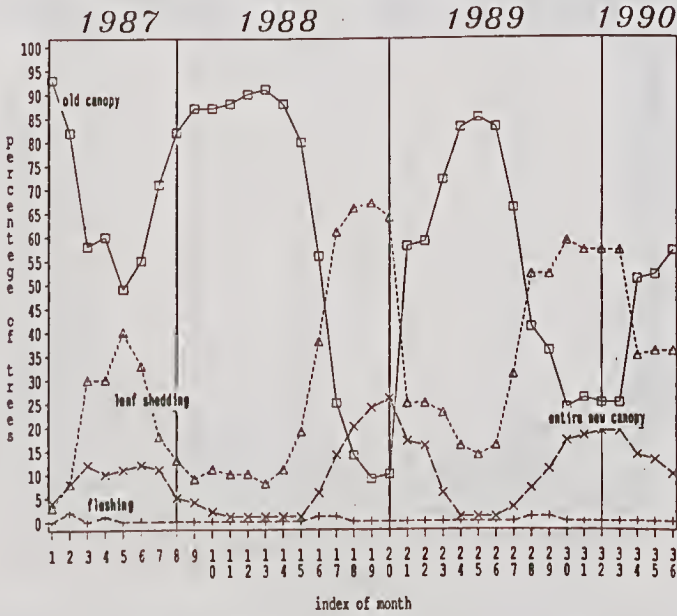


Figure 15 - Combined vegetative phenologies of the eight forest communities studied.

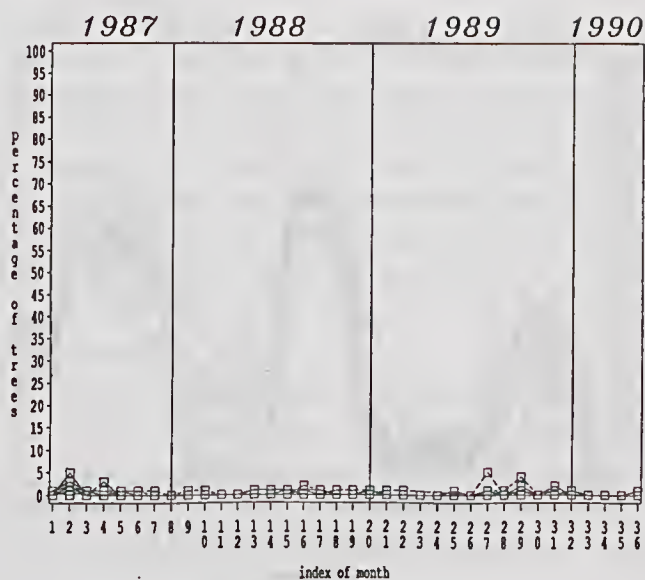


Figure 16 - Percentage of trees showing the phase of flushing in the eight forest communities studied.

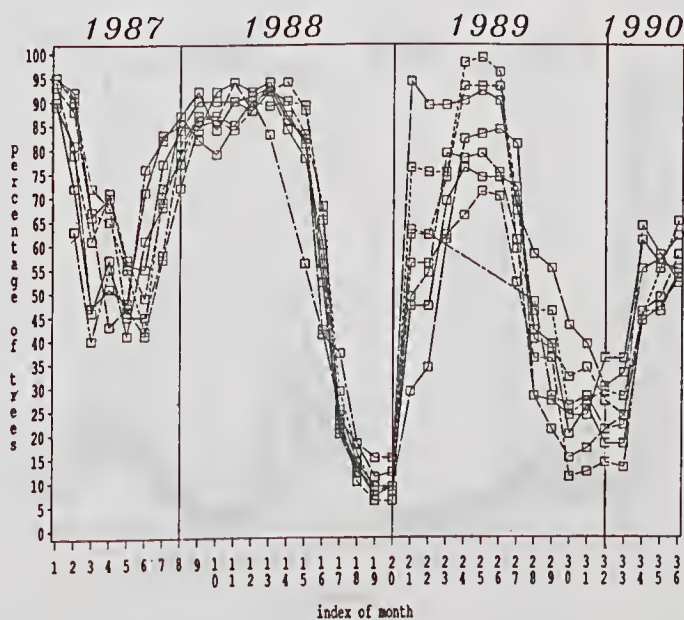


Figure 17 - Percentage of trees showing the phase of old canopy in the eight forest communities studied.

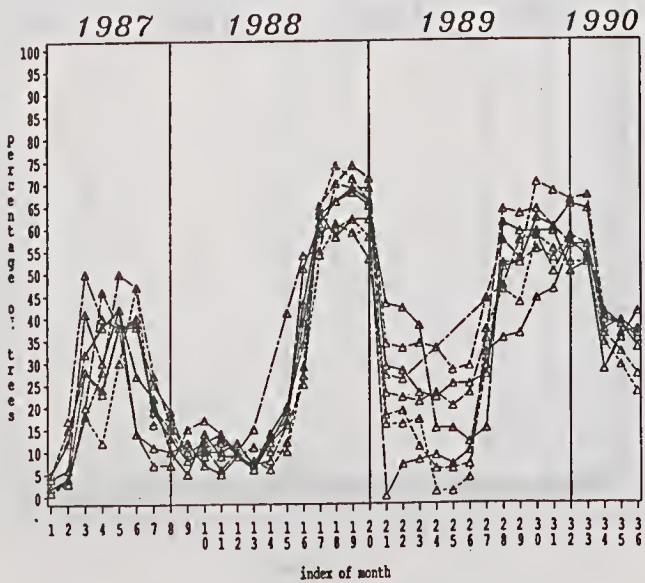


Figure 18 - Percentage of trees showing the phase of Leaf shedding in the eight forest communities studied.

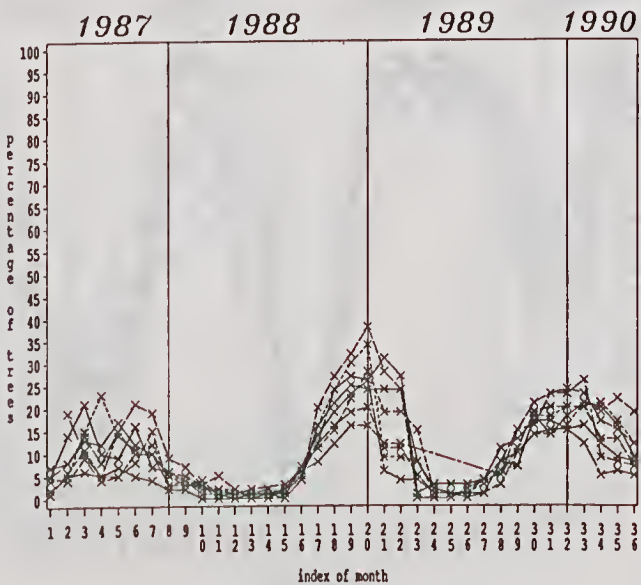


Figure 19 - Percentage of trees showing the phase of entire new canopy in the eight forest communities studied.



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Appendix 1. Number of genera, species and trees studied.

FAMILY	Nº GENERA	Nº SPECIES	Nº TREES
ANACARDIACEAE	4	9	75
BOMBACACEAE	5	7	25
BURSERACEAE	3	26	323
CARYOCARACEAE	1	4	27
CHRYSOBALANACEAE	4	23	213
CONNARACEAE	1	1	9
HUMIRIACEAE	4	4	87
LECYTHIDACEAE	6	15	143
LEGUMINOSAE - MIM.	8	20	275
MELIACEAE	4	12	70
MYRISTICACEAE	2	3	89
PALMAE	2	2	25
QUIINACEAE	2	2	7
SIMAROUBACEAE	2	2	13
VOCHYSIACEAE	3	7	94
Sub Total	51	137	1475
MISCELLANEOUS*	-	22	33
Total	-	-	1508

* Not included in the species study.

Appendix 2. List of the species studied

A paper describing the phenology of each of the following species mentioned with derived mathematical models is yet to be published but a list of the species studied is given below.

ANACARDIACEAE

Anacardium giganteum Hancock ex Engler

Anacardium spruceanum Benthham

Astronium obliquum Griseb.

Spondias mombin L.

Tapirira guianensis Aublet



Tapirira peckoltiana Engler

Tapirira sp. nov.

Thyrsodium guianense Sagot ex March.

Thyrsodium spruceanum Bentham

BOMBACACEAE

Bombacopsis nervosa (Uitt.) A. Robyns

Eriotheca crassa (Uitt.) A. Robyns

Eriotheca globosa (Aublet) A. Robyns

Eriotheca surinamensis (Uitt.) A. Robyns

Pachira aquatica Aublet

Pseudobombax munguba (Mart. & Zucc.) Dugand

Quararibea guianensis Aublet

BURSERACEAE

Protium altsonii Sandw.

Protium apiculatum Swart vel aff.

Protium cuneatum Swart

Protium decandrum (Aublet) Marchand

Protium giganteum Engler

Protium guianense (Aublet) Marchand

Protium cf. *mori* Daly

Protium nitidifolium (Cuatr.) Daly

Protium opacum Swart cf. subsp. *rabelianum* Daly

Protium pallidum Cuatr.

Protium paniculatum Engler

Protium polybotryum (Turcz.) Engler

Protium robustum (Swartz) Poster

Protium sagotianum Marchand

Protium strumosum Daly

Protium subserratum (Engl.) Engler

Protium tenuifolium Engler

Protium trifoliolatum Engler

Protium sp. nov. 1

Protium sp. nov. 2 (*P.* aff. *unifolium*)

Protium sp. nov. 3

Tetragastris altissima (Aubl.) Swartz

Tetragastris hostmannii (Engl.) O'Kuntze



Tetragastris panamensis (Engler) O'Kuntze

Trattinickia burseraefolia Mart.

Trattinickia glaziovii Swart

CARYOCARACEAE

Caryocar glabrum (Aublet) Pers.

Caryocar microcarpum Ducke

Caryocar villosum (Aublet) Pers.

Caryocar pallidum A.C. Smith

CHRYSOBALANACEAE

Couepia guianensis Aublet

Couepia joaquinae Prance

Couepia robusta Huber

Hirtella bicornis Mart. & Zucc. s.sp. *pubescens* Ducke

Hirtella eriantra Benth

Hirtella obidensis Ducke

Hirtella piresii Prance

Licania apetala (E.Mey.) Fritsch

Licania canescens R. Ben

Licania egleri Prance

Licania heteromorpha Benth var. *heteromorpha* Prance

Licania impressa Prance

Licania kunthiana Hook f.

Licania laevigata Prance

Licania latifolia Benth ex Hook.

Licania macrophylla Benth

Licania micrantha Miq.

Licania minutiflora (Sagot) Fritsch

Licania octandra (Hoff. ex R. & S.) Kuntze

Licania pallida Spruce ex Sagot

Licania robusta Sagot

Licania silvae Prance

Parinari excelsa Sabine

CONNARACEAE

Connarus perrottetii (DC.) Planchon



HUMIRIACEAE

- Endopleura uchi* (Huber) Cuatr.
Humiria balsamifera (Aubl.) J. St. Hil.
Saccoglottis guianensis Benth
Vantanea parviflora Aublet

LECYTHIDACEAE

- Bertholletia excelsa* H. & B.
Couratari guianensis Aublet
Couratari oblongifolia Ducke & Knuth
Couroupita guianensis Aublet
Eschweilera amazonica R. Knuth
Eschweilera coriacea (A.P. DC.) Mart. ex Berg
Eschweilera grandiflora (Aublet) Sandwith
Eschweilera obversa (Berg.) Miers
Eschweilera pedicellata (Richard) Mori
Eschweilera sp. nov. 1
Gustavia augusta L.
Gustavia hexapetala (Aublet) J.E. Smith
Lecythis corrugata Poiteau subsp. *corrugata* Mori
Lecythis idatimon Aublet
Lecythis lurida (Miers) Mori

LEGUMINOSAE / MIMOSOIDAE

- Cedrelinga cateniformis* (Ducke) Ducke
Dinizia excelsa Ducke
Inga acrocephala Steud.
Inga alba (Sw.) Willd.
Inga capitata Desv.
Inga edulis Mart.
Inga cf. *negrensis* Benth
Inga cf. *panurensis* Spruce ex Benth
Inga paraensis Ducke
Inga pezizifera Benth
Inga rubiginosa (Rich.) DC.
Inga thibaudiana DC.



Inga sp.nov. 1

Marmaroxylon racemosum (Ducke) Killip

Parkia decussata Ducke

Parkia oppositifolia Benth

Parkia ulei (Harms.) Kuhlman

Pentaclethra macroloba (Willd.) Kuntze

Piptadenia communis Benth

Zygia ampla (Spruce ex Benth.) Pittier

MELIACEAE

Carapa guianensis Aublet

Cedrela odorata L.

Guarea kunthiana A. Juss.

Guarea macrophylla Vahl s.sp. *pachycarpa* (C.DC.) Penn.

Guarea pubescens (Rich.) A. Juss.

Guarea purusana C.DC.

Trichilia cf. *hirta* L.

Trichilia lecointei Ducke

Trichilia micrantha Benth

Trichilia quadrijuga Kunth s.sp. *quadrijuga* Penn.

Trichilia schomburgkii C. DC.

Trichilia septentrionalis C.DC.

MYRISTICACEAE

Iryanthera sagotiana (Benth) Warb.

Virola flexuosa A.C.Smith

Virola michelii Heckel

PALMAE

Oenocarpus bacaba Mart.

Socratea exorrhiza (Mart.) H. Wendl.

QUIINACEAE

Quina aff. *longifolia* Spruce ex Pl. & Tr.

Touroulia guianensis Aublet

SIMAROUBACEAE

Sinaba cedron Planchon

Sinarauba amara Aublet



VOCHYSIACEAE

Erismia laurifolium Warm.

Erismia sp. nov. 1

Qualea albiflora Warm.

Qualea cf. *coerulea* Aubl.

Qualea paraensis Ducke

Vochysia obscura Warm.

Vochysia vismiifolia Spruce ex Warm.

MISCELLANEOUS. Observation of 32 marked trees originally misidentified were excluded from the species study mentioned but included in the community study of this paper. A list is given below.

DICHAPETALACEAE

Tapura amazonica Poepp. & Endl. s.sp. *manausensis* Prance

EUPHORBIACEAE

Mabea caudata Pax & K. Hoffm.

Pera bicolor (Klotzsch) Muell. Arg.

LACISTEMATACEAE

Lacistema aggregatum (Bergius) Rusby

LAURACEAE

Mezilaurus lindaviana Schw. & Mez ex Glaziou

Ocotea cf. *duplocolorata* Vattimo-Gil

LEGUMINOSAE / CAESALPINIOIDEAE

Dialium guianense (Aubl.) Sandw.

Hymenaea intermedia Ducke

Macrobium acaciaefolium Benth

LEGUMINOSAE / MIMOSOIDEAE

Strypnodendron paniculatum Poepp. & Endler

LEGUMINOSAE / PAPILIONOIDEAE

Bowdichia nitida Benth

Hymenolobium sericeum Ducke



MELASTOMATACEAE

Miconia surinamensis Gleason

NYCTAGINACEAE

Neea constricta Spruce ex Schmidt

OCHNACEAE

Ouratea olivaeformis Engler

RUBIACEAE

Ferdinandusa elliptica Pohl

SAPINDACEAE

Cupania hirsuta Radlk. aff. *C. scrobiculata* Rich.

Toulicia acutifolia Radlk.

SAPOTACEAE

Pouteria sp.

Micropholis venulosa (Mart. & Eichler) Pierre

TILIACEAE

Apeiba burchellii Sprague

Mollia lepidota Spruce ex Bentham

UNKNOWN: 9 trees of unknown species

